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Extreme site fidelity as an optimal strategy in an unpredictable and homogeneous environment

Running Head: Gunnison sage-grouse site fidelity.

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Abstract

1. Animal site fidelity structures space-use, population demography, and ultimately gene flow. Understanding the adaptive selection for site fidelity patterns provides a mechanistic understanding to both spatial and population processes. This can be
achieved by linking space-use with environmental variability (spatial and temporal) and demographic parameters. However, rarely is the environmental context that drives the selection for site fidelity behavior fully considered.

2. We use ecological theory to understand whether the spatial and temporal variability in breeding site quality can explain the site fidelity behavior and demographic patterns of Gunnison sage-grouse (*Centrocercus minimus*). We examined female site fidelity patterns across multiple spatial scales: proximity of consecutive year nest locations, space-use overlap within and across the breeding and brooding season, and fidelity to a breeding patch. We also examined the spatial and temporal variability in nest, chick, juvenile, and adult survival.

3. We found Gunnison sage-grouse to be site faithful to their breeding patch, area of use within the patch, and generally to where they nest, suggesting an ‘Always Stay’ site fidelity strategy. This is an optimal evolutionary strategy when site quality is unpredictable. Further, we found limited spatial variability in survival within age groups, suggesting little demographic benefit to moving among patches. We suggest Gunnison sage-grouse site fidelity is driven by the unpredictability of predation in a relatively homogeneous environment, the lack of benefits and likely costs to moving across landscape patches and leaving known lek and breeding/brooding areas.

4. Space use and demography are commonly studied separately. More so, site fidelity patterns are rarely framed in the context of ecological theory, beyond questions related to the win-stay:lose-switch rule. To move beyond describing patterns and understand the adaptive selection driving species movements and their demographic consequences requires integrating movement, demography, and environmental variability in a synthetic framework.

5. Site fidelity theory provides a coherent framework to simultaneously investigate the spatial and population ecology of animal populations. Using it to frame ecological
questions will lead to a more mechanistic understanding of animal movement, spatial
population structuring, and meta-population dynamics.

Key-words: animal movement; Gunnison sage-grouse; nest success; radio-telemetry; site
fidelity theory; space-use; survival; win-stay:lose-switch.

Introduction
The spatial context of where and how species survive and reproduce is a fundamental
component of their life history and ecology. A commonly observed behavior among animal
species is the repeated use of distinct spatial areas in one or more seasons or stages of their
life history (e.g., birds and mammals: Greenwood 1980; Lewis 1995; Hoover 2003, fishes:
molluscs: Lind 1989, reptiles: Broderick et al. 2007, insects: ?). The ubiquity of animals
having fidelity to certain spatial areas suggests it is an evolutionary adaptive strategy in
which individuals incur benefits from familiarity with their physical and social environment
(Piper 2011). Site familiarity benefits and proximate causes of ‘site fidelity’ include efficient
resource acquisition (Olsson et al. 2010), successful deterring of competitors (i.e., “resident
advantage”; Jakobsson 1988), efficient movements and use of micro-environments (Vlasak
2006), effective predator avoidance (Brown 2001), and decreased conflict with neighbors
(Stamps 1987).

The evidence for fitness or demographic benefits of site fidelity has historically
been limited (Piper 2011), but increasing (e.g., Lafontaine et al. 2017; Patrick &
Weimerskirch 2017). Site fidelity is an emergent property of individual’s spatially
restricting their movements to only certain areas. This restriction ultimately influences the
population’s distribution and abundance and can structure meta-populations via
immigration/emigration (Schmidt 2004; Matthiopoulos et al. 2005); lifetime space use
patterns influence gene flow and thus evolutionary processes (Sugg 1996). Commonly, site
fidelity studies have focused on natal philopatry and breeding area fidelity because they
have high fitness consequences (Schmidt et al. 2010). There has also been considerable
focus on the evolutionary context and mechanisms driving natal dispersal (Mattysen 2012).
However, it is increasingly appreciated that site fidelity, regardless of natal area, is an
important process across time periods and activities outside the breeding season (Piper
2011; Northrup et al. 2016; Patrick & Weimerskirch 2017) and may drive individual-based
habitat associations for many years (McIntyre et al. 2017).

An individual’s decision to remain faithful to its breeding area has often been
linked to their past breeding experience (Hoover 2003; Schmidt 2004). This suggests
individuals use their experiences to assess breeding site quality (Schmidt 2001). A simple
decision rule that is widely supported across animal taxa (especially birds; Piper 2008) is
that of the win-stay:lose-switch (WSLS) rule (Schmidt 2004): individuals return to a
breeding site if they successfully produce young or switch breeding sites if they are
unsuccessful. The type of information used in this decision is known as ‘private
information’ (Schmidt et al. 2010). An alternative decision process is based on the
perceived social information from neighboring individuals (Doligez et al. 2002; Piper 2011).
Social information helps average over the stochasticity inherent in individual breeding
success (as in the WSLS rule). The context of when private or social information may be
advantageous, and more generally when site fidelity may be an evolutionary adaptive
strategy, can be understood via the ecology of information theory (Schmidt et al. 2010).

The ecology of information theory frames breeding site fidelity decisions in terms
of the spatial and temporal variability of the resources that affect breeding success (Switzer
1997; Schmidt 2001; Schmidt et al. 2010; Table 1). Areas with high temporal variation
provide little information (private or social) about breeding site quality, thus we expect
breeding site decisions to be independent of past breeding experience (Schmidt et al. 2010).
Furthermore, when there is low spatial variation in site quality within and among habitat
patches (collection of possible breeding sites), regardless of temporal variability, we expect
an always-stay decision rule to be optimal when there are costs to moving (Switzer 1997).

In contrast, if there is high spatial variation that is not temporally variable (thus predictable site quality), breeding experience provides valuable information about site quality and thus aids in the choice among available sites. In these environments, we should expect species to adopt a WSLS site fidelity strategy at either the site or habitat patch level (Schmidt et al. 2010). If site quality within a habitat patch varies more strongly than across patches, individuals benefit from being faithful at the site-level depending on their own breeding success (i.e., WSLS-Site, decision using private information). However, if site quality varies more among habitat patches than within a patch, individuals benefit by having high fidelity to the habitat patch. Thus, we should expect an individual to move among patches based on the breeding success of individuals within the patch (i.e., WSLS-Patch, decision via social information).

Despite site fidelity and the WSLS rule being commonly examined in animal ecology, rarely are patterns evaluated in the context of theoretical expectations based on spatial and temporal variation in site quality. Even more so, we are unaware of site fidelity studies that consider the spatial constraints from a species' mating system, such as lekking. Lekking is a common mating system among birds and insects, in which males aggregate at distinct locations to display for females and obtain reproductive opportunities. The aggregation of both males and females have potential spatial constraints to where individuals subsequently nest, forage, incubate eggs, and brood chicks.

We used the Gunnison sage-grouse (*Centrocercus minimus*) to examine site fidelity behavior across multiple scales in the context of theoretical expectations based on the spatial and temporal variation in breeding site quality, and spatial constraints of their lek mating system. The Gunnison sage-grouse is a recently recognized species (Young et al. 2000) occurring in the sagebrush (*Artemisia* spp.) habitats of southwestern Colorado and southeastern Utah, USA. The species was recently listed as federally threatened (USFWS 2014). They are known to use different types of seasonal habitat throughout the annual
cycle, generally defined as the breeding (mating, nesting), brooding (rearing chicks), and winter seasons (Rice et al. 2017). We used a multi-year dataset (2004-2010) to examine site fidelity patterns and the influence of nest success across multiple scales: proximity of consecutive year nest locations, space-use overlap within the breeding season, and fidelity to a breeding patch. We also examined space-use fidelity within and across the brooding season, but without reliable measures of brood success, we did not link brooding area fidelity to demographic outcomes. Furthermore, we considered whether there are benefits to moving among breeding patches by examining the spatial and temporal variation in chick (<30 days), juvenile (>30 days to 1 year), and yearling/adult (>1 year) survival.

Our objectives were to 1) characterize regional breeding patches and movement, 2) describe environmental spatial and temporal variability within and among breeding patches, 3) evaluate indirect evidence of spatial and temporal variability in breeding patch quality by examining seasonal range size, and 4) evaluate direct evidence by examining spatial and temporal variation in nest, chick, juvenile, and yearling/adult survival of Gunnison sage-grouse. These findings improved our understanding of the spatial demography of Gunnison sage-grouse and adaptive selection of these patterns.

We hypothesized Gunnison sage-grouse have high fidelity to a breeding patch, but not to specific nest sites within the patch (Fisher et al. 1993). Individuals are typically faithful to a lek or a lek complex (group of nearby leks; Connelly et al. 2011) and commonly nest within the same area as their lek (Gunnison sage-grouse: average of 2-4 km; Young et al. 2015). We did not expect Gunnison sage-grouse to be faithful to nest locations (Fisher et al. 1993).
Materials and methods

Study Area

We studied Gunnison sage-grouse (hereafter, sage-grouse) in the eastern portion of the Gunnison basin (Gunnison and Saguache counties, Colorado, USA). The basin comprise 85–90% of the species’ range, covered approximately 2,000 km², and occurred between an elevation of 2,300 and 2,900 m. The study area was predominately sagebrush steppe, dominated by mountain big sagebrush (Artemisia tridentate) interspersed with rabbitbrush (Chrysothamnus spp.), antelope bitterbrush (Purshia tridentata), serviceberry (Amelanchier spp.), and mountain snowberry (Symphoricarpos oreophilus).

Capture and Monitoring

We captured sage-grouse from March to early May between 2004 and 2010 using spot-lighting techniques (Wakkinen et al. 1992; Giesen et al. 1982). We fit birds with a 17 g necklace-style VHF radio-transmitter (model A4050 by Advanced Telemetry systems or model R12B by Holohil Systems, Ltd.) equipped with a 4-h mortality sensor. The transmitter was <2% of the weight of an average sage-grouse (female: 1270 g SD 90 g). Each radio-marked bird was relocated using hand-held antennas once every 1-3 days throughout the breeding (1 April - 15 July) and brooding seasons (16 July to 30 September; Rice et al. 2017). Observers were trained to maximize the accuracy of azimuths while considering constraints, such as private property. Each relocation included recording multiple azimuths (≥2) from known locations, typically within 30 minutes or less. Relocating individuals occurred throughout the day (0800-1700 hrs.). A female was determined to be nesting if found in the same location for more than 3 consecutive days. Visual observations of females on nests were avoided to minimize disturbance. After a female left the nest, the nest was located to assess the fate of the eggs (e.g., hatched, depredated, abandoned, or unknown) and a vegetation survey was conducted (Davis et al.
Sagebrush and grass cover and height surrounding the nest was surveyed using 30 m transects, centered at the nest; vegetation cover and height was estimated at 5 m intervals along the transect. A Daubenmire frame (20 x 50 cm) was used to visually estimate the percent grass and forb cover.

**Breeding Patch and Environmental Variability**

We defined breeding patches based on *a priori* regional knowledge of breeding area affiliations separated by natural boundaries, including habitat and elevation (which covary with land-use patterns, such as agriculture and development; Fig. 1; see Appendix S1 in Supporting Information). Each patch consists of multiple leks. It is at this scale that we examined site fidelity within and among patches. The six breeding patches are South Parlin, North Parlin, Signal Mountain, Flat Top, Ohio Creek, and Chance Gulch (Fig. 1).

**Spatial and Temporal Variation in Breeding Site Quality**

Historical sage-grouse habitat consisted of large expanses of contiguous sagebrush, which are relatively stable ecosystems at the time scale of annual breeding site decision making. The dominant landscape scale disturbances were fire and herbivory from bison (*Bos bison*); fire rotation intervals were typically $\geq 100$ years (Bukowski and Baker 2013) and grazing from large nomadic bison populations were likely highly temporally and spatially heterogeneous (Chambers et al. 2016). The relative temporal stability of these ecosystems would suggest annual correlation and thus predictability of site quality, at least at the scale relevant for selection processes of site fidelity via WSLS.

We considered environmental spatial variability within and among breeding patches by examining spatial patterns in nest site vegetation, annual precipitation, and soils. To understand whether there was greater variability in vegetation within or among patches, we fit a hierarchical Bayesian log-linear regression model to vegetation collected at nest sites. For each vegetation measure observed (shrub and grass cover and height; $y_{i,s}$) at
nest $i$ in breeding patch $s$, we estimated a mean ($\mu_s$) and variance ($\sigma^2_s$) for each breeding patch, where $\log(y_{i,s}) \sim \text{Normal}(\mu_s, \sigma^2_s)$ and $\mu_s$ are patch-level random effects ($\mu_s \sim \text{Normal}(\mu_1, \tau^2)$). If $\tau^2 > \sigma^2_s$, there is more spatial variation across breeding patches than within patch $s$. We fit a similar model to investigate the variability in rainfall patterns (PRISM 30-Year Normals from 1981-2010; Resolution: 0.92 km x 0.72 km; PRISM 2017) at estimated sage-grouse locations (details provided below) within and across breeding patches. For each model, we used diffuse priors and fit the model using Markov Chain Monte Carlo (MCMC) methods. Last, we estimated the probability of sage-grouse locations belonging to a set of dominant soil moisture-temperature regimes using a multinomial log-linear model in the R package ‘nnet’. Soil data were compiled by Maestas et al. 2016 (Resolution: 0.01 km x 0.01 km). Variation in soil regimes provide indirect support to variation in dominant vegetation characteristics and their resistant/resilient properties (Chambers et al. 2016), and thus variation in breeding patch quality.

Measuring site quality is difficult due to the complexity of interacting environmental factors. Therefore, we examined variation in sage-grouse seasonal ranging across breeding patches as an indirect measure of patch quality. Intraspecific variation in range size can be understood in the context of optimal foraging theory, which predicts that animals will maximize energy intake while minimizing energetic expenditures, such as movement (Pyke et al. 1977; Northrup et al. 2016). Thus, individuals in areas of greater forage quality and quantity should use smaller areas. We examined seasonal range size by estimating the 95% isopleth of individuals’ utilization distribution within the breeding and brooding seasons (estimation details are described in the ‘Site Fidelity’ section). We quantify variation by estimating the semi-interquartile range ($\frac{(Q_3 - Q_1)}{2}$) for each season and patch, as well as across patches. If the within patch semi-interquartile range was less than across patches, we considered there to be less variation within the patch.
To understand whether site and patch environmental variability translates into breeding area quality variability, we examined the spatial and temporal factors that are hypothesized to influence nest success (see Davis et al. 2015a). Specifically, we investigated nest site vegetation characteristics (shrub height, shrub cover, grass cover, and grass height), breeding patch affiliation, temporal factors (e.g., year, timing of incubation initiation, and nest age), and age of the nesting female (yearling or adult). We used a predictive modeling framework that optimizes within-sample predictive performance using cross-validation. Specifically, we fit the nest success data (1 = success, 0 = failure) using a logistic regression model with all standardized covariates that was optimized using the least absolute shrinkage and selection operator (LASSO; Tibshirani 1996). We used 5-fold cross validation, evaluating shrinkage parameters using the average deviance (-2 × log-likelihood) of the left out data across all folds. LASSO regularizes model parameters, thereby accommodating numerical issues due to multicollinearity of covariates and providing variable selection by removing effects of covariates. The result is an optimal predictive model that is coherently interpretable in terms of important ecological effects (see Gerber et al. 2015; Hooten & Hobbs 2015). We used the same procedure to model nest success as a multinominal outcome to evaluate whether predation on nesting females or eggs drives nest failure and whether it varied spatially or temporally (0 = nest failed or was abandoned, 1 = nest failed due to the female or eggs being depredated, 2 = nest success). Predation could make quality nest site selection highly unpredictable and thus may affect female site fidelity. We conducted model fitting optimization and cross-validation for both analyses in the R package ‘glmnet’ (Friedman et al. 2010).

We further considered variation in breeding site quality by evaluating the spatial and temporal variation in chick, juvenile, and yearling/adult survival across breeding patches.
by extending previous analyses of these populations (Davis et al. 2015b, 2016). We used the most parsimonious models of these analyses and include additional individual covariates indicating the breeding patch location of the individual. We evaluated temporal and spatial survival differences by comparing models using AIC, BIC, and likelihood ratio tests, and estimating the expected marginal differences between breeding patch coefficients (e.g., $\hat{\beta}_{\text{diff}} = \hat{\beta}_1 - \hat{\beta}_2$ with variance $\text{Var}(\hat{\beta}_1) + \text{Var}(\hat{\beta}_2) - 2\text{Cov}(\hat{\beta}_1, \hat{\beta}_2)$, where Cov is the covariance).

**Site Fidelity**

**Nest site fidelity**

We investigated nest site fidelity by examining whether individuals switch nesting locations among breeding patches and whether this occurred after nest failure in the previous year. We also estimated the Euclidean distance between consecutive year nesting locations and evaluated whether female sage-grouse are more likely to nest close to a previous nest location if they were successful in hatching eggs in the previous year. We analyzed data using a Bayesian log-linear regression model that included a single variable (NestSuccess) indicating whether the previous years nest was successful or not; priors on parameters were diffuse. We fit the model using MCMC and made inference based on posterior distributions. If individuals showed fidelity to a successful nest location in the previous year, we assumed that there were demographic benefits, possibly due to site familiarity. To evaluate whether this was the case, we modeled whether nest success was different in the second year depending on whether an individual was successful or not in the first year. We analysed these data using a Bayesian logistic regression model with a single variable indicating whether the first year was successful or not (NestSuccessYear1).
Breeding and brooding space-use and patch fidelity

To understand whether female sage-grouse used the same breeding patches and sites across years, we used telemetry data to simultaneously estimate animal locations along with individual breeding and brooding season utilization distributions for each year. Breeding utilization distributions correspond to activities after leaving the lek, during the nesting period. We modeled the telemetry data using a recently developed Bayesian Azimuthal Telemetry Model (ATM; Gerber et al. 2018) that properly accounts for spatial location uncertainty within the utilization distributions. For each radio-tagged individual \((l = 1, ..., L)\) that is relocated on certain days \((i = 1, ..., N_l)\) within each season/year, an observer records a set of azimuths \((\theta_{lij}; j = 1, ..., J_{li})\) at known locations \(z_{lij} \equiv (z_{1lij}, z_{2lij})'\) to estimate the sage-grouse’s spatial location, \(\mu_{li} \equiv (\mu_{1li}, \mu_{2li})'\). We used the von Mises distribution and a link function to relate the true animal location with the data,

\[
\text{Observation Process: } \theta_{lij} \sim \text{von Mises}(\tilde{\theta}_{lij}, \kappa_{li}), \\
\text{Link Function: } \tilde{\theta}_{lij} = \tan^{-1}\left(\frac{\mu_{2li} - z_{2lij}}{\mu_{1li} - z_{1lij}}\right).
\]

(1)

The parameter \(\kappa\) is an estimate of azimuthal uncertainty, recognizing that the location of each bird is not known exactly; simulations based on the sage-grouse data indicated good statistical properties for estimating \(\kappa\) and thus coverage of the true animal location (Gerber et al. 2018). We used the estimated spatial locations \((\mu_{li})\) along with a small number of aerial and known locations, in a non-parametric kernel density estimator (Hooten et al. 2017) to derive each individuals season/year utilization distribution. Aerial locations were taken with a GPS during low-altitude flights that circled the bird’s location. We assumed these locations were not known exactly by treating them as multivariate normal distributed, centered at the aerial location coordinates with a covariance matrix \(12.5^2 I\); this allowed a maximum deviation from the GPS location of approximately 50 m.

For an individual that was relocated \(n\) times (a minimum of 10 locations) within a season/year, we estimated their seasonal utilization distribution for the \(k^{th}\) MCMC
iteration using the 95% isopleth of the kernel function,

\[
\hat{f}(c) = \sum_{i=1}^{n} \frac{g((c_1 - \mu_1^{(k)})/b_1)g((c_2 - \mu_2^{(k)})b_1)}{nb_1^2},
\]

evaluated at the locations \( c \equiv (c_1, c_2)' \), kernel function \( g(\cdot) \), and bandwidth parameter \( b_1 \).

To measure breeding and brooding area site fidelity, we compared individuals’ utilization probability distribution (UD) across seasons (breeding-breeding, brooding-brooding, breeding-brooding) and years. The UDs correspond to the post-lekking period. For each comparison, we measured site fidelity as a degree of overlap between UDs using the Bhattacharyya coefficient (Bhattacharyya 1943). For probability distributions \( p \) and \( q \) over the same domain \( X \), the Bhattacharyya coefficient is defined as,

\[
BC(p, q) = \sum_{x \in X} \sqrt{p(x)q(x)},
\]

where \( 0 \leq BC \leq 1 \). BC will be approximately zero when there is no overlap and one when there is complete overlap. Therefore, a BC value of zero could indicate an individual used a different patch between years or the same patch, but different sites within a patch. To clarify how individuals’ space-use varies across and within breeding patches, we summarized results by BC value and breeding patch association for each UD comparison.

Last, we investigated the proximity of individuals’ space-use by estimating the Euclidean distance between the highest UD densities being compared. We compared different sets of overlap in UDs to provide general and specific insights into site fidelity behavior by comparing 1) among all UDs within and across seasons (breeding-breeding, brooding-brooding, and breeding-brooding) for consecutive and non-consecutive years, and 2) within breeding season by nest success. Since the number of spatial locations varied across individuals by season and year (10 to 54), we evaluated the consistency in our results by comparing inference from using all the location data and standardizing the number of locations to only 10 per individual by season and year.
Results

Capture and Monitoring

A total of 94 female sage-grouse were relocated in at least two seasons with a minimum of 10 locations per season between 2004 and 2010 (see Appendix S2 in Supporting Information Appendix 2, Table A1). We observed a total of 23,869 azimuths across all individuals, which were used to estimate 6,057 locations of female sage-grouse. The number of azimuths observed per relocation varied, ranging from 2 to 12 (Appendix 1, Fig. A1). Including aerial and known locations, we obtained a total of 6,608 sage-grouse locations. The number of locations for each individual observed in a season/year ranged from 10 to 54 with a median of 21.

Each individual was observed from 2 to 11 seasons with a median of 3 seasons. The majority of individuals during the breeding season were only observed within a single breeding patch (81%). Fifteen individuals were observed in two patches and two were observed in three patches; these multi-patch observations were a small number of each individuals’ location data (<5%), except for one individual that had 142 locations split between two patches. Individuals observed at multiple patches were not limited to only using adjacent patches. The majority of individuals during the brooding season (89%) were also only observed within a single patch; four individuals were only observed once at a second patch, while two individuals were observed at more than one patch, primarily in different years.

Spatial variation in breeding site quality

We found that vegetation characteristics were more variable within a breeding patch than across patches (Appendix 1, Fig. A2). In contrast, we found considerably more variation in annual precipitation across patches than within (Appendix 1, Fig. A3). We also found that sage-grouse locations dominantly occurred within frigid-ustic (cold-intermediate moisture)
and cryic-udic (cool-moist) soils (Appendix 1, Fig. A4). These soil regimes typify elevated productivity within shrub-steppe communities (Chambers et al. 2016). While the dominant soil types were generally similar across the breeding patches (Appendix 1, Fig. A4), a model allowing the probabilities to vary across soil types ($M_{soil}$) had better predictive ability with the data (measured by AIC) than a model that considered them constant ($M_{null}$; $\Delta AIC_{M_{soil}} = 0$, $\Delta AIC_{M_{null}} = 15069.57$).

We found noticeable variation in ranging area across breeding patches by season, suggesting patch-level variation in quality (Figs. 2, A5-A6). Variation in UD area across patches was generally greater in the breeding season than the brooding season. Median patch-level ranging size in the breeding season was lowest at Ohio Creek and Flat Top ($\approx 2.9$ km$^2$) and larger at Chance Gulch (5.60 km$^2$) and South Parlin (8.0 km$^2$). Signal Mountain UD areas were even larger at a median of 12.30 km$^2$ and largest at North Parlin with a median of 16.40 km$^2$. North Parlin was much more variable across breeding patches in the breeding season compared to within season, while the other patches were similar or less variable (Appendix 1, Figs. A5-A6). Based on optimal foraging theory, we would expect Ohio Creek and Flat Top to have a higher nest success, given the reduced energetic expenditure related to movement. Brooding season UD areas were smaller or equivalent in size to breeding season UD areas. Median UD areas were smallest at Flat Top (2.46 km$^2$), then Ohio Creek and South Parlin ($\approx 3.57$ km$^2$), then Signal Mountain and Chance Gulch ($\approx 4.89$ km$^2$), and were largest at North Parlin (9.61 km$^2$). Within patch variation in the brooding season was greater than across patch variation only at North Parlin and Flat Top (Appendix 1, Figs. A5-A6).

**Spatial and temporal variation in nest success**

We observed a total of 177 nests belonging to 120 individuals. We found no support for any covariates hypothesized to influence nest success and failure (Appendix 1, Fig. A7). The optimal predictive model indicated a mean nest success of 0.446 ± 0.038 SE. We also
found no support for any covariates hypothesized to influence nest failure, predation, and
nest success (Appendix 1, Fig. A8). The optimal predictive model indicated a mean nest
failure, predation, and success of 0.070, 0.462, and 0.468, respectively.

Spatial and temporal variation in survival

We found little evidence to suggest there was annual variation in chick, juvenile, or
adult/yearling survival, however, there was a fair amount of parametric uncertainty (Davis
et al. 2015b, 2016; Appendix 1, Tables A1-A3 and subsection ‘Spatial and temporal
variation in survival’). We also found relatively minimal variation in survival of the
different age groups by breeding patch (Appendix 1, Tables A1-5; Fig. A9). Among all
pairwise comparisons, we found chick survival was much higher (comparing maximum
likelihood estimates) at Ohio Creek than Signal Mtn. and North Parlin (Appendix 1, Table
A4). In the juvenile survival analysis, we found North Parlin had higher survival than
South Parlin. All other comparisons were not statistically significant; detecting differences
that were not extreme was difficult due to high parameter uncertainty. Last, adult survival
was generally similar among breeding patches (Appendix 1, Fig. A9). However, we did find
that Ohio Creek survival was marginally lower than North Parlin and Chance Gulch. Also,
South Parlin survival was lower than North Parlin and Chance Gulch (Appendix 1, Table
A4).

Nest site fidelity

Out of 43 individual sage-grouse with multiple years of nesting location data (consecutive
years and not, range of 2-4 years per individual), only a single individual was observed to
nest in more than one breeding patch. This individual was observed nesting in one patch in
2005 and 2006 and a different patch in 2008 and 2010; in all years, this individual was
successful at hatching chicks. Among 47 consecutive year nesting comparisons, (36 unique
individuals) no birds were observed to switch breeding patch; 19 out of 47 were
unsuccessful in the previous year, but did not switch their patch. We found support for a negative effect \( P(\beta_{\text{NestSuccess}} < 0) = 0.96; E[\beta_{\text{NestSuccess}}] = -0.713, -1.45 \text{ to } 0.073, 95\% \text{ credible interval} \) of nest success on the distance between consecutive year nest locations (Fig. 3). The median distance between nest locations when individuals were previously unsuccessful at hatching chicks was 357 m (209 - 598, 95\% credible interval), which decreased when individuals were successful to 178 m (113 - 276, 95\% credible interval). However, we found no improvement in nest success in the second year based on the first year nest success \( P(\beta_{\text{NestSuccessYear1}} > 0) = 0.26; E[\beta_{\text{NestSuccessYear1}}] = -0.404, -1.60 \text{ to } 0.790, 95\% \text{ credible interval} \).

**Breeding and brooding space-use and patch fidelity**

First, we found no changes in our inference to breeding and brooding space-use and patch fidelity between using all individuals’ spatial locations and when standardizing the sample size (see Appendix 1). We found strong fidelity of individuals to their patch during both the breeding and brooding seasons (Appendix 1, Fig. A10; >0.91 proportion of individuals used the same patch across all comparisons). Comparing consecutive year space-use in the breeding season, only a single individual (total of 46 comparisons) was observed to use two different patches. During the brooding season, only two individuals (total of 57 comparisons) were observed to use different patches in consecutive years (one of these individuals was also observed in different patches during the breeding season). Comparing across consecutive and non-consecutive years also supports strong site fidelity to the patch; 95\% and 91\% of all comparisons were within the same patch for the breeding and brooding season, respectively (73 and 90 total comparisons; Appendix 1, Fig. A10).

We found seasonal space-use overlap was variable, but consistently showed moderate overlap for all comparisons (Fig. 4; Appendix 1, Fig. A11). Notably, it was uncommon for an individual to use the same breeding patch (within or across seasons), but have no overlap in their space-use (i.e., BC value of 0). This was especially rare when
comparing within seasons. The median space-use overlap was highest within the breeding
season, then the brooding season, then across these seasons (Fig. 4; Appendix 1, Fig. A11).
The average Euclidean distance between UDs across all seasons and years was around 2 to
3 km (Appendix 1, Fig. A12). The median Euclidean distance across breeding seasons was
commonly between 0 and 1 km, but ranged up to 6 km, while the average distance across
brooding seasons was commonly 0 to 2.5 km, but ranged up to 10 km. As such, most
individuals use the same breeding patch for breeding and brooding across all years and
generally use the same area within each season and somewhat across seasons.

We also found no indication that female sage-grouse move sites within the
breeding season based on their previous nesting experience (Fig. 5; Appendix 1, Fig. A13).
Across all comparisons, there was moderate spatial overlap regardless of nest success
outcome. In fact, we found higher median overlap among consecutive years when a
previous nest had failed. This result was also supported by a slightly lower median distance
between UDs when a previous nest had failed (Appendix 1, Fig. A14). However, space-use
overlap was moderate even when comparing across non-consecutive years by nest success,
suggesting individuals simply use a similar area regardless of nesting outcome (Fig. 5). We
also found moderate space-use overlap across brooding seasons and between
breeding-brooding seasons (median BC values of $\approx 0.45$; Figs. A15-A16). The median
Euclidean distance between UDs across brooding season was 2 km, while between breeding
to brooding seasons was slightly higher at 2.5 km (Figs. A17-A18).

**Discussion**

Rarely are site fidelity patterns framed in the context of relevant ecological theory, beyond
questions related to the WSLS strategy. Site fidelity behavior and its influence on
demography and movement can be understood in the context of environmental spatial and
temporal variability (Schmidt et al. 2010). This allows a more mechanistic understanding
of habitat selection across spatial scales (Lafontaine et al. 2017), as well as possible
metapopulation dynamics by recognizing the level of connectivity among habitat patches (Switzer 1997), which has important implications for population regulation (Matthiopoulos et al. 2005) and persistence (Schmidt 2004). More so, empirical studies framed by theory are essential to modifying the theory and its predictions based on new discoveries and previously unconsidered conditions and constraints.

In this study, we quantified female Gunnison sage-grouse site fidelity across multiple spatial scales, framing observations based on theorized drivers of spatial and temporal variability in breeding site quality. We found Gunnison sage-grouse to exhibit high site fidelity across spatial scales. Individuals were faithful to their breeding patch, area of use within their patch by season, and typically nested near their previous nesting location, using private information of their previous nest success outcome to decide the proximity (mean distance of 0.18 when successful and 0.36 km when unsuccessful).

However, there was no support that this nest-level WSLS rule is beneficial, as nesting closer to a previously successful nest did not improve the likelihood of success in the following year. However, we recognize that nest site selection may be based on variables that were not collected in this study, including brooding or fledgling success.

Despite the extreme site fidelity observed, we also found environmental variation across and within breeding patches, which suggests variation in site quality. Specifically, we found across patch variation in soil temperature-moisture regimes, precipitation, and generally the ranging size of UDs within the breeding season. We recognize that range size as a measure of site quality is a simplification of a complex behavioral movement process; we encourage future studies to focus on finer-scale movement as a means to better understand costs and benefits of movement. In terms of structural vegetation differences, we generally found more variability among sites within patches than across patches. However, despite these suggestive differences in site quality, we found no strong evidence of spatial (within or among patch) or temporal variation in nest success or chick, juvenile, and yearling/adult survival.
Without clear spatial variation in breeding site quality, there is no benefit to moving sites at any spatial scale. Our observations of nest site vegetation were all within optimal ranges according to habitat management guidelines for Gunnison sage-grouse (Davis et al. 2015a). Moreover, we found no evidence that nest failure due to the eggs or the female being depredated varied spatially or temporally. Nest failure due to predation was as likely as for the nest to be successful. It is believed that predation is the primary cause of mortality of all age classes of Gunnison sage-grouse (Young et al. 2015). This suggests that, while site quality may be predictable in terms of structural vegetation characteristics, it is unpredictable in terms of predation. Even when individuals were successful and subsequently nested in the following year closer to their previous nest (i.e., following a WSLS strategy), there was no evidence of improved nest success. Individuals may simply be unable to cue in on sites to reduce nest predation, and thus live in a homogenous and unpredictable environment. Furthermore, we found weak spatial variation in survival of all age groups among patches, suggesting why sage-grouse may only rarely move patches.

Lekking birds are believed to have some of the highest levels of nest predation (Phillips 1990), and from experimental studies, there is strong evidence that predation pressure and predator hunting mode fundamentally affects prey movement and space-use (Miller et al. 2014). But also, breeding site fidelity strategy is known to depend on the specific cause of reproductive failure (Schmidt 2001). In considering the diverse predators of sage-grouse (includes birds of prey, corvids, and terrestrial mammals), which are typically wide-ranging generalists that likely take eggs and birds opportunistically (Hagen 2011; Young et al. 2015; Conover & Roberts 2017), there may be nowhere to escape the possibility of predation. Therefore, in relatively homogenous habitat, in which individuals may be unable to avoid numerous opportunistic predators or assess breeding site quality in terms of predation pressure, the costs of movement may easily supersede any benefit, selecting individuals with extreme site fidelity. In fact, an always stay site fidelity strategy,
in which individuals do not use WSLS, is the evolutionary optimal strategy in
unpredictable homogenous environments (Switzer 1997; Schmidt et al. 2010). Furthermore,
minimizing movement, especially flying, is complementary with the behavioral and
phenotypic selection for crypsis in sage-grouse. Despite being strong fliers, sage-grouse are
mostly ground-dwelling, relying on camouflage until they are threatened and resort to
flying (Young et al. 2015).

However, predation may not fully explain why Gunnison sage-grouse do not
move among breeding patches. We might expect Gunnison sage-grouse to selectively move
among patches in response to failed nesting due to nest predation because moving farther
(across patches, rather than within) may be more likely to change predator communities
and abundance, and thus predation pressure. Further, site fidelity to the patch may be
partially a by-product of fidelity to a lek or lek complex. Fidelity to leks and lek proximity
to nesting is well documented in sage-grouse populations (Connelly et al. 2011; Young et al.
2015), including in this study population. However, we were unable to link space-use with
specific lek locations, as we may not have observed all leks used by each individual. The
selection pressure to nest within the general proximity to their lek and thus the costs of
moving breeding patches is less clear. Patch-level variation may be irrelevant in site fidelity
patterns and thus potential social information also irrelevant. Perhaps though, the diversity
of ground and aerial predators in the sagebrush steppe has led to the selection against
moving among patches to limit exposure to predation, and also because the ubiquity of
opportunistic nest predators means that movements of any scale are irrelevant to altering
nest predation pressure (as observed in this study). An additional factor that may explain
the lack of long distance movements of Gunnison sage-grouse could be due to physiological
constraints on grouse and generally all Galliformes. Galliformes are known to have flight
muscles that are almost exclusively glycolytic muscle fibers, which limits flights to short
bursts of activity before quickly fatiguing (Butler 2016). Therefore, to move long distances
may require several short flight bursts, which are energetically costly and perhaps risky by
attracting the attention of predators. Last, we can not rule out that site fidelity may be at least partially due to a lack of density-dependent factors that when present would cause individuals to disperse rather than compete for limited resources (Harts et al. 2016).

**Consequences of site-fidelity**

Spatial segregation of subgroups by breeding patch affiliation within the eastern portion of the Gunnison basin suggests a high-level of spatial structuring. Over a seven year period, we observed few movements across breeding patches, suggesting that immigration-emigration processes have minimal influence on the meta-population dynamics among patches. Rather, within breeding patch dynamics in the breeding and brooding season are likely to drive changes in the abundance of this threatened bird. Theoretical results also suggest that high site fidelity of aggregated breeding species (e.g., lek or colonial breeders) can hinder population growth by reducing the colonization of unoccupied habitat, such that only a portion of the available habitat is occupied (Matthiopoulos et al. 2005). We suggest habitat changes from anthropogenic and natural disturbances should be viewed in the context of the spatial scale of the breeding patches. Since all realistic landscape disturbances (i.e., fire and development) are smaller in spatial scale than the Gunnison Basin, it is arguable that the breeding patches afford a measure of population redundancy. Thus, environmental and anthropogenic change within one breeding patch is unlikely to affect birds associated with other breeding patches. However, the extent of movement among patches within the winter is still unknown. Further, we were not able to explicitly evaluate juvenile natal dispersal, which for many species occurs at higher rates than breeding dispersal (Harts et al. 2016).

**Conclusions**

Animal site fidelity is a commonly observed behavior that has important consequences to animal space-use and thus the spatial structuring of populations. Examining the spatial
and temporal variability of environmental and demographic outcomes contributed to the understanding of ecological processes likely driving Gunnison sage-grouse demography and site-fidelity patterns. Notably, their always-stay strategy suggests higher fitness outcomes by minimizing movements and capitalizing on site familiarity benefits in an environment where nest predation is ubiquitous, breeding/brooding habitat is generally suitable, demographic benefits to moving are minimal, and moving may incur higher predation risk. Given the extreme site fidelity observed in this study, future population and habitat management could be framed in the context of these spatial affiliations.

REFERENCES


Supplementary Material

Appendix 1: Additional study details and results tables and figures.

Appendix 2: Data summary table of the number of locations and azimuths of Gunnison sage-grouse by year and season.

Acknowledgments

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions of the U.S. Fish and Wildlife Service employees in this article are their own and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Funding was provided by CPW 1701 and NSF DMS 1614392 awards. Trapping and handling protocols were approved by the Colorado Parks and Wildlife Animal Care and Use Committee (permit # 02-2005). M. L. Phillips led the Gunnison sage-grouse field data collection effort.

Data Accessibility

Data are archived at Dryad (DOI pending review). Location data are not publicly available due to concerns of providing detailed spatial information on a federally threatened species. Data requests can be made at Colorado Parks and Wildlife with Dr. James Gammonley, jim.gammonley@state.co.us.
Author Contributions

- BDG, MBH, CPP, MBR, JHG, ADA, and AJD conceived the ideas and contributed to critical editing of previous drafts and gave final approval for publication.

- BDG, MBH, CPP designed the statistical framework and fit the data.

- BDG led the writing of the manuscript.
Table 1: Theoretical optimal site fidelity predictions depending on temporal and spatial variability in site quality.

<table>
<thead>
<tr>
<th>Temporal Variation</th>
<th>Spatial Variation</th>
<th>Information</th>
<th>Site Fidelity Prediction</th>
</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td>Site ≡ Patch</td>
<td>None</td>
<td>Always Stay³</td>
</tr>
<tr>
<td>High</td>
<td>Site &gt; Patch</td>
<td>None</td>
<td>No Fidelity - move among sites, rather than patches, regardless of breeding success</td>
</tr>
<tr>
<td>High</td>
<td>Patch &gt; Site</td>
<td>None</td>
<td>No Fidelity - move among patches, rather than sites, regardless of breeding success</td>
</tr>
<tr>
<td>Low</td>
<td>Site ≡ Patch</td>
<td>None</td>
<td>Always Stay³</td>
</tr>
<tr>
<td>Low</td>
<td>Site &gt; Patch</td>
<td>Private</td>
<td>Fidelity to Site (WSLS-Site)</td>
</tr>
<tr>
<td>Low</td>
<td>Patch &gt; Site</td>
<td>Social</td>
<td>Fidelity to Patch (WSLS-Patch)</td>
</tr>
</tbody>
</table>

¹Sites are locations within a patch.
³Assuming there are costs to moving. Otherwise, individuals are expected to move following an ideal-free settlement strategy, thus indifferent to the site/patch or past experience (Schmidt 2001).
Figure 1: Elevation (top plot) and vegetation (middle plot) classification throughout the Gunnison sage-grouse critical habitat in the Gunnison basin of Colorado, USA. Point estimate locations (bottom plot) for all individuals tracked from 2004-2010 during the breeding and brooding seasons were assigned to a breeding area affiliation (top plot).
Figure 2: Summary plots of posterior median estimates of individual Gunnison sage-grouse’ 95% utilization distribution area for the breeding and brooding seasons by breeding area patch. The symbol * indicates measurements beyond the maximum y-axis limit. Individual estimates along with 95% credible intervals can be found in Appendix 1, Fig. A6.
Figure 3: Posterior distributions of mean distance (left plot) and nest success effect (on the log-scale; right plot) between consecutive year nest locations of Gunnison sage-grouse.
Figure 4: Summary plots of the posterior median space-use overlap (Bhattacharyya Coefficient) among all comparisons (consecutive and non-consecutive years) within individual sage-grouse by season and whether the utilization distribution occurred in the same breeding patch or different breeding patches. Individual estimates and associated 95% credible intervals can be found in Appendix 1, Fig. A11.
Figure 5: Summary plots of the posterior median Bhattacharyya coefficient estimates of space-use overlap across breeding seasons by nesting success for consecutive and non-consecutive years. Individual estimates and associated 95% credible intervals can be found in Appendix 1, Figure A13.